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Gibberellin-Producing *Promicromonospora* sp. SE188 Improves *Solanum lycopersicum* Plant Growth and Influences Endogenous Plant Hormones[§]

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Plant growth-promoting rhizobacteria (PGPR) producing gibberellins (GAs) can be beneficial to plant growth and development. In the present study, we isolated and screened a new strain of *Promicromonospora* sp., SE188, isolated from soil. *Promicromonospora* sp. SE188 secreted GAs into its growth medium and exhibited phosphate solubilization potential. The PGPR produced physiologically active (GA_1 and GA_4) and inactive (GA_9, GA_{12}, GA_{19}, GA_{20}, GA_{24}, GA_{34}, and GA_{53}) GAs in various quantities detected by GC/MS-SIM. *Solanum lycopersicum* (tomato) plants inoculated with *Promicromonospora* sp. SE188 showed a significantly higher shoot length and biomass as compared to controls where PGPR-free nutrient broth (NB) and distilled water (DW) were applied to plants. The presence of *Promicromonospora* sp. SE188 significantly up-regulated the non C-13 hydroxylation GA biosynthesis pathway (GA_{12}→GA_{24}→GA_9→GA_4→GA_{34}) in the tomato plants as compared to the NB and DW control plants. Abscisic acid, a plant stress hormone, was significantly down-regulated in the presence of *Promicromonospora* sp. SE188. Contrarily, salicylic acid was significantly higher in the tomato plant after *Promicromonospora* sp. SE188 inoculation as compared to the controls. *Promicromonospora* sp. SE188 showed promising stimulation of tomato plant growth. From the results it appears that *Promicromonospora* sp. SE188 has potential as a bio-fertilizer and should be more broadly tested in field trials for higher crop production in eco-friendly farming systems.

***Keywords*:** gibberellins, plant growth-promotion, *Solanum lycopersicum*, *Promicromonospora* sp. SE188

Introduction

The rhizosphere is a rich source of various microorganisms that can benefit plant growth and survival. Rhizospheric bacteria are widely known to improve plant growth. These beneficial rhizobacteria play a pivotal function by (i) supplying essential nutrients, (ii) secreting bioactive plant growth regulators, (iii) mediating various biotic and abiotic stress conditions, and (iv) improving soil structure (Hayat *et al.*, 2010) for the plants. They also compete with pathogens for nutrients or a specific niche on the root and induce systemic resistance (Bloemberg and Lugtenber, 2001). The increase in the human population, and consequent demands for higher crop production and increased food supply, has persuaded farmers to use synthetic fertilizers. Meeting the food demands by using synthetic fertilizers has not only affected the long-term fertility of agricultural lands but has also paved the way for the development of numerous environmental problems. Presently, various biological approaches have been assessed and used to improve crop growth and yield.

Plant growth-promoting rhizobacteria (PGPR) offer a valid alternative to chemical fertilizers, herbicides, and pesticides but their effectiveness often lacks consistency (Bevivino *et al.*, 1998). To achieve the goal of sustainable crop production, the microbial symbiosis in the rhizosphere can play a crucial role not only in enhanced plant growth but also in counteracting various biotic and abiotic stresses (Rodriguez and Fraga, 1999; Sturz and Nowak, 2000; Sturz *et al.*, 2000; Şahin *et al.*, 2004; Zaidi *et al.*, 2008; Shoebitz *et al.*, 2009; Adesemoye *et al.*, 2009; Lugtenberg and Kamilova, 2009; Khan *et al.*, 2011a, 2011b, 2011c). A variety of PGPRs such as *Bacillus*, *Enterobacter*, *Burkholderia*, *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillium*, *Azotobacter*, *Beijerinckia*, *Erwinia*, *Flavobacterium*, *Rhizobium*, and *Serratia* are now being used worldwide with the aim of enhancing plant productivity (Burd *et al.*, 2000; Cocking, 2003). These PGPRs stimulate plant growth and enhance plant biomass (Adesemoye *et al.*, 2009; Lugtenberg and Kamilova, 2009). The beneficial effects of PGPRs have been demonstrated for many agricultural crop species such as wheat (Khalid *et al.*, 2004), tobacco (Kloepper *et al.*, 1991; Zhang *et al.*, 2004), *Brassica juncea* (Asghar *et al.*, 2002) tomatoes (Kidoglu *et al.*, 2008), bell

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peppers and cucumbers (Kidoglu *et al*., 2008) and barley (Çakmakçi *et al*., 2007). The crop growth-promotion has been correlated with the ability of PGPRs to produce various bioactive substances such as plant hormones (gibberellins) and secondary metabolites (Hayat *et al*., 2010; Kang *et al*., 2010).

Gibberellins (GAs) are ubiquitous plant hormones that elicit various metabolic functions required during a plant's growth such as seed germination, stem elongation, sex expression, flowering, the formation of fruits and senescence (Hedden, 1997; Hedden and Kamiya, 1997). Phytohormone-producing PGPR associations with crop plants provide additional support in maintaining growth and development of the host plant (Joo *et al*., 2004, 2005, 2009; Kang *et al*., 2009, 2010). Previous studies (Atzorn *et al*., 1988; Bottini *et al*., 1989; Janzen *et al*., 1992; Mansour *et al*., 1994; Bastián *et al*., 1998; Gutiérrez-Mañero *et al*., 2001; Joo *et al*., 2004, 2005, 2009; Kang *et al*., 2009, 2010) have elucidated the GA-production capability of PGPR. However, *Promicromonospora* have yet to be classified as a PGPR. We could not find any report related to *Promicromonospora* sp. regarding the production of plant hormones and the promotion of plant growth.

In the present study, we elucidated the GA-production potential a newly isolated rhizobacterium *Promicromonospora* sp.. It was collected from a field soil sample and screened for its potential to produce GAs and solubilize tricalcium phosphate. The *Promicromonospora* sp. was applied to tomato plants and the effect on biosynthesis of endogenous GAs, abscisic acid and salicylic acid were evaluated in order to understand its effects on plant physiology and metabolism.

Materials and Methods

Promicromonospora sp. SE188 and tomato growth

The bacterial isolate SE188 was identified as a new strain on the basis of the partial 16S ribosomal DNA (rDNA) sequence. The chromosomal DNA was isolated through standard procedures (Sambrook and Russel, 2001). The almost complete 16S rDNAs were PCR amplified using the 27F primer; 5′-AGAGTTTGATC (AC) TGGCTCAG-3′ and 1492R primer; 5′-CGG (CT) TACCTTGTTACGACTT-3′, which were complementary to the 5′ end and 3′ end of the prokaryotic 16S rDNA, respectively. The amplification reaction was performed as previously described (Adachi *et al*., 1996). SE188 was identified as a strain of *Promicromonospora* sp. The bacterial culture suspension of *Promicromonospora* sp. was incubated for 3 days at 30°C on a shaking incubator at 200 rpm in broth medium. The bacterial suspension was diluted in sterile distilled water to a final concentration of 10^8 CFU/ml. Tomato seeds were purchased from Seminis Korea Co. (Korea), surface sterilized with sodium hypochlorite (5%) for 10 min, and thoroughly rinsed with autoclaved double distilled water (DDW). Seeds were sown in plastic pots containing horticultural soil under controlled greenhouse conditions (30±2°C). The composition of horticultural soil was as fallow; peat moss (13–18%), perlite (7–11%), coco-peat (63–68%) and zeolite (6–8%), with macro-nutrients being NH_4^+~90 mg/kg; NO_3^-~205 mg/kg; P_2O_5~350 mg/kg and K_2O~100 mg/kg (autoclaved three times). Two-week-old tomato seedlings (15 per treatments) were treated with 5 ml of bacterial culture suspension, and the growth attributes i.e., shoot and root length, dry weights, number of leaves and chlorophyll content were recorded after two weeks of treatment. Double distilled water (DDW) and nutrient broth (NB) were used as two negative controls. Each treatment had fifteen plants and the experiment was repeated three times. The chlorophyll contents of all fully expanded leaves were analyzed with a Chlorophyll meter (Minolta Co., Ltd, Japan). The phosphate solubilization and nitrogen contents of the tomato shoots were determined as described by Kang *et al.* (2010).

Extraction and quantification of gibberellins

To characterize the GAs secreted into the pure bacterial culture, the bacteria were inoculated into nutrient broth (120 ml) for 7 days at 30°C (shaking incubator-120 rpm) as described previously (Kang *et al*., 2010). The culture medium and bacterial cells were separated by centrifugation (2,500×g at 4°C for 15 min). The culture medium (50 ml) was used to extract and purify the GAs as described by Kang *et al.* (2009). Before purification, deuterated GA internal standards (20 ng; [17, 17-$^2H_2$] GA_1, GA_4, GA_{12}, GA_{19}, GA_{24}, GA_{34}, and GA_{53}) were added to the culture filtrate (CF). Tritiated GAs i.e. [1, 2-$^3H_2$] GA_9 and [1,2-$^3H_2$] GA_{20} were also added (obtained from Prof. Lewis N. Mander, Australian National University, Canberra, Australia). About 20 ng each of deuterated [17, 17-$^2H_2$] GA_{34}, GA_9, GA_{12}, GA_4, and GA_{24} internal standards were added. The extract of the CF and the plants were chromatographed on a 3.9×300 m Bondapak C18 column (Waters Corp., USA) and eluted at 1.5 ml/min with the following gradients: 0 to 5 min, isocratic 28% MeOH in 1% aqueous acetic acid; 5 to 35 min, linear gradient from 28% to 86% MeOH; 35 to 36 min, 86% to 100% MeOH; 36 to 40 min, isocratic 100% MeOH. Forty-eight fractions of 1.5 ml each were collected (Supplementary data Table S1). The fractions were then prepared for gas chromatography/mass spectrometry (GC/MS) with selected ion monitoring (SIM) (6890N Network GC System, and 5973 Network Mass Selective Detector; Agilent Technologies, USA) (Supplementary data Table S1). For each GA, 1 µl of sample was injected into a 30 m×0.25 mm i.d., 0.25 µm film thickness DB-1 capillary column (J and W Scientific Co., USA). The GC oven temperature was programmed for a 1 min hold at 60°C, and then to rise at 15°C/min to 200°C followed by 5°C/min to 285°C. Helium carrier gas was maintained at a head pressure of 30 kPa. The GC was directly interfaced to a mass selective detector with an interface and source temperature of 280°C, an ionizing voltage of 70 eV, and a dwell time of 100 ms. Full-scan mode (the first trial) and the three major ions of the supplemented [$^2H_2$] GA internal standards as well as the sample GAs were monitored simultaneously. The retention time was determined using hydrocarbon standards to calculate the KRI (Kovats Retention Index) value and the GAs quantification was based on the peak area ratios of the non-deuterated (extracted) GAs to the deuterated GAs (Supplementary data Table S1). The detection limit was 20 pg/ml for the bacterial culture. The data was calculated in ng/ml (bacterial culture) or ng/g (plants) and the analyses were repeated three times.

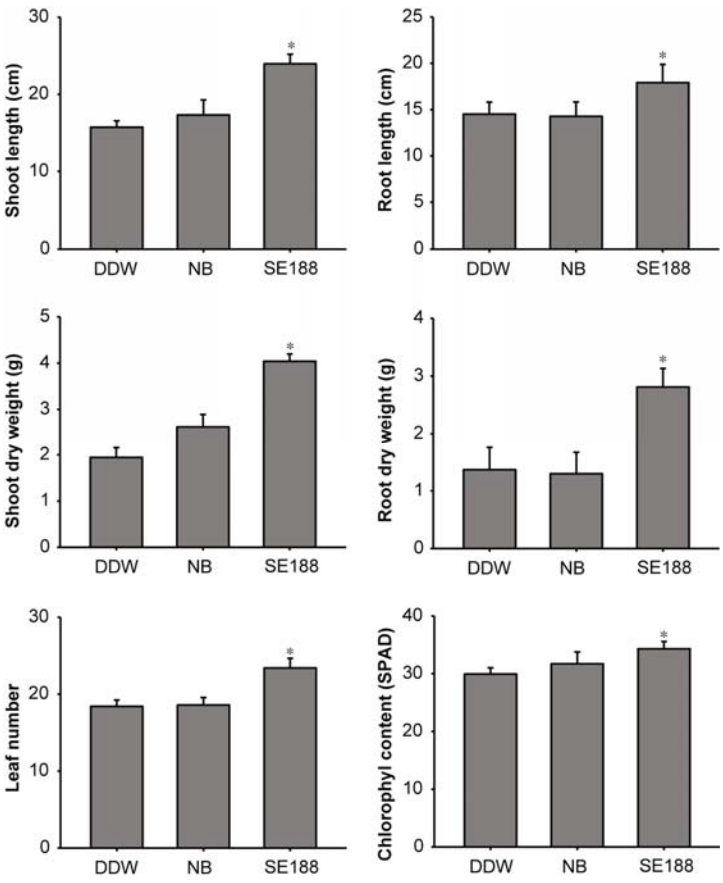
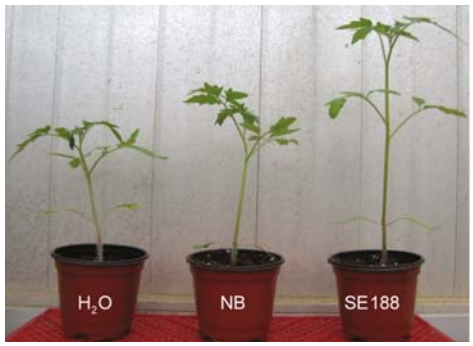


Fig. 1. Effect of *Promicromonospora* sp. (SE188) culture application on tomato plant growth and its allied attributes. Double distilled water (DDW) and nutrient broth (NB) were used as controls. The '*' indicates that the SE188 treatments are significantly different (P<0.05) from the DDW and NB as evaluated by Student t-test. SPAD in the chlorophyll content refers to 'Soil Plant Analysis Development'. The error bar shows the mean values±standard deviation (n=15).



Analysis of endogenous ABA and SA contents

The endogenous ABA was extracted according to the method of Qi *et al.* (1998). The extracts were dried and methylated by adding diazomethane. Analyses were done using a GC-MS SIM (6890N network GC system, and 5973 network mass selective detector; Agilent Technologies, USA). For quantification, the Lab-Base (ThermoQuset, UK) data system software was used to monitor responses to ions of m/z 162 and 190 for Me-ABA and 166 and 194 for Me-[$^2H_6$]-ABA (Supplementary data Table S2).

SA was extracted and quantified as described previously (Seskar *et al.*, 1998). Briefly, freeze-dried leaf tissue samples were ground to a powder and 0.1 g was sequentially extracted with 90–100% methanol by centrifuging at 10,000×g. The combined methanol extracts were vacuum dried. Dry pellets were re-suspended in 2.5 ml of 5% trichloroacetic acid. The supernatant was partitioned with ethyl acetate: cyclopentane: isopropanol (100:99:1, v/v). The top organic layer containing free SA was transferred to a 4 ml vial and dried with nitrogen gas. The dry SA was suspended in 1 ml of 70% methanol. High Performance Liquid Chromatography (HPLC) analyses were carried out on a Shimadzu instrument with a fluorescence detector (Shimdzu RF-10AXL, excitation and emission 305–365 nm respectively), fitted with a C18 reverse-phase HPLC column (HP hypersil ODS, particle size 5 µm, pore size Waters) (Supplementary data Table S3). The flow rate was 1.0 ml/min.

Statistical analysis

The data was analyzed for standard error using Graphpad Prism (5.0) and Student's t-test was used to identify significant values. The mean values were compared using Duncan's Multiple Range Tests at P≤0.05 (ANOVA SAS release 9.1; SAS Cary, USA).

Results

Isolation of bacteria promoting tomato plant growth

Promicromonospora sp. SE188 was initially isolated from agricultural-field soil samples taken on Jeju Island, Republic of Korea. Initially, 891 bacterial strains isolated from field soil were screened for GA production and phosphate solubilization. Among the isolated bacterial strains, *Promicromonospora* sp. SE188 showed promising results (Supplementary data Table S3). The details of some of the most active strains bearing phosphate solubilization potential have been given in the supplementary data (Supplementary data Table S3). The 16S rDNA sequence of bacterial isolate SE188 showed a 99% similarity with *Promicromonospora* sp. and was thus identified as *Promicromonospora* sp. SE188. To assess the effect of *Promicromonospora* sp. SE188 on plant growth and allied growth attributes, its culture was applied to tomato plants for two weeks. The *Promicromonospora* sp.

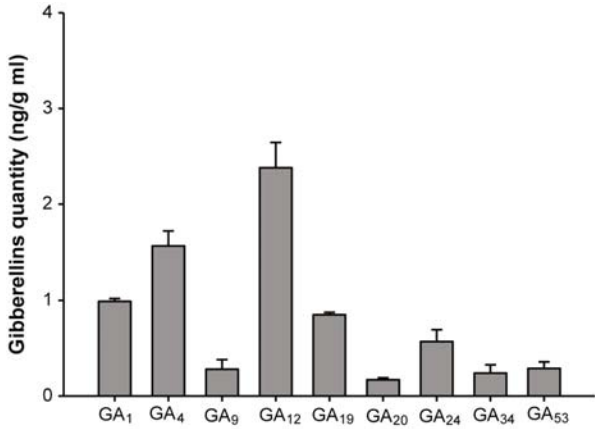


Fig. 2. Gibberellin quantification for a culture of *Promicromonospora* sp. (SE188). The analysis was undertaken according to Kang *et al.* (2009) and the experiment was repeated three times.

application significantly increased the shoot length of the tomato plants as compared to the controls (NB and DDW) (Fig. 1). Similarly, the roots of the tomato plants that had been treated with the bacterial culture were significantly longer than the NB and DDW controls. Secondary and tertiary root formation was more prominent in the treated plants than the controls. The tomato shoot and root biomass was significantly higher in plants inoculated with *Promicromonospora* sp. than in the non-inoculated control (NB and DDW) plants. The number of leaves and the chlorophyll content were also significantly higher in *Promicromonospora* sp. treated plants than in the control plants (Fig. 1).

Gibberellin analysis in the *Promicromonospora* sp. SE188 culture

After five days growth of *Promicromonospora* sp. in the NB culture medium (at 30°C; 200 rpm), the culture was ultracentrifuged (at 4°C; 5,000×g) to obtain a clear supernatant (50 ml). The supernatant was extracted and chromatographed for the detection of gibberellins (GAs). The GC/MS–SIM analysis detected various physiologically active and inactive GAs in different quantities (Fig. 2). Physiologically bioactive GAs included GA_1 (0.99±0.03 ng/ml) and GA_4 (1.58±0.11 ng/ml). Physiologically inactive GAs were GA_9 (0.2±0.04 ng/ml), GA_{12} (2.38±0.11 ng/ml), GA_{19} (0.85±0.07 ng/ml), GA_{20} (0.17±0.08 ng/ml), GA_{24} (0.57±0.07 ng/ml), GA_{34} (0.24 ±0.03 ng/ml), and GA_{53} (0.29±0.02 ng/ml). The amounts of GA_{12} and GA_4 were significantly higher as compared to other GAs. No GAs were detected in un-inoculated NB medium.

Phosphate solubilization capacity of *Promicromonospora* sp. SE188

The insoluble tricalcium phosphate solubilization capacity of *Promicromonospora* sp. SE188 was low until 72 h of incubation, but after 96 h, the clearing zone increased appreciably. At 96 h, the solubilization radius was significantly larger (Fig. 3). The pH, on the other hand, was low at 96 h, during the phosphate solubilization process (Fig. 3).

Analysis of endogenous gibberellin content

The endogenous gibberellin contents of the tomato plants were analyzed by GC/MS SIM to assess the effect of *Promicromonospora* sp. (SE188) culture application on GA biosynthesis, using NB and water as controls. *Promicromonospora* sp. SE188 application significantly activated GA biosynthesis pathways in the tomato plants as compared to medium alone (NB) or water (DDW) (Fig. 4). Physiologically active GA_4 content was significantly ($P<0.05$) higher in treated culture as compared to the DDW control. The GA_4 content was not significantly different in the NB and DDW controls (Fig. 4). The content of GA_9 was significantly higher in treated plants as compared to DDW control plants, while GA_9 content was the same in the NB and DDW control plants. The GA_{12} content was significantly activated in *Promicromonospora* sp. treated plants compared to the DDW and NB control plants. In DDW and NB control plants, the GA_{12} content was not

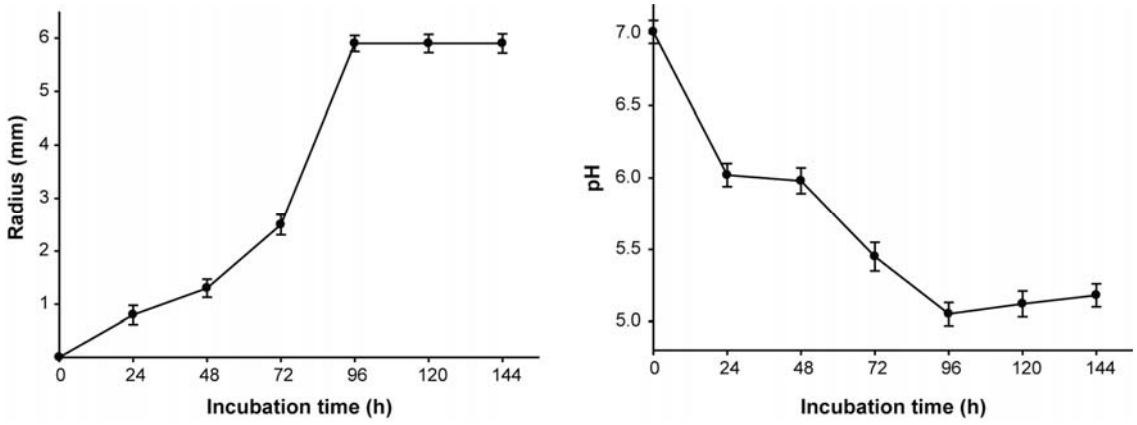


Fig. 3. Phosphate solubilization capacity and its associated pH for *Promicromonospora* sp. SE188, inoculated on the National Botanical Research Institute's Phosphate (NBRIP) growth medium plates ((Nautiyal, 1999). The radius on the plate is the zone of solubilization. In a separate experiment using liquid NBRIP medium for bacterial growth, P solubilization was confirmed by checking the pH of the media on a daily basis. A decline in pH of the medium was observed up to 96 h. Values given are the means of three replicates.

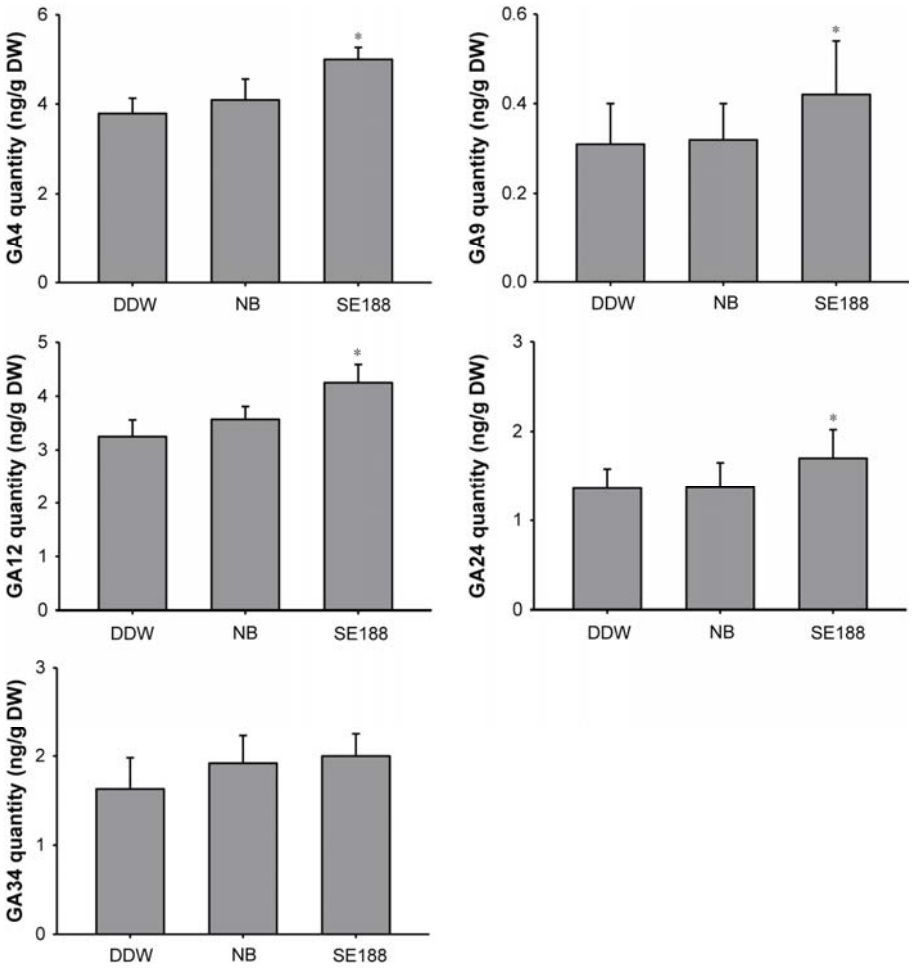


Fig. 4. Effect of *Promicromonospora* sp. (SE188) culture treatment on the gibberellin (GAs) biosynthesis of tomato plants. Double distilled water (DDW) and bacteria-free nutrient broth (NB) were used as controls. The '*' indicates that the SE188 treatments were significantly different ($P<0.05$) than the DDW as evaluated by Student t-test. The error bar shows mean values ±standard deviation (n=3).

significantly different. The same trend was also recorded for the GA_{24} in bacterial culture treated plants compared to DDW and NB control plants. The GA_{24} content in plants treated with the bacterial culture was almost the same as in the DDW and NB controls and the GA_{34} content was not significantly different from the DDW and NB control plants (Fig. 4).

Analysis of endogenous ABA and SA content

The endogenous abscisic acid (ABA) content was significantly reduced in *Promicromonospora* sp. treated plants as com-

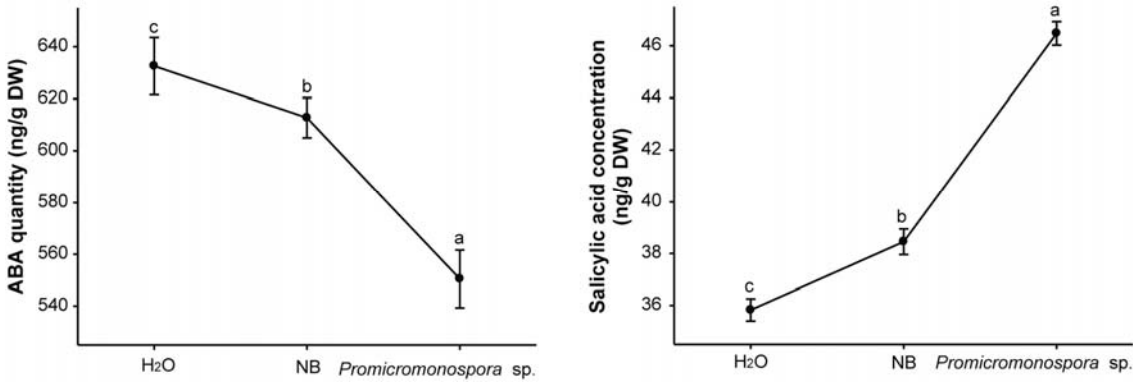


Fig. 5. Effect of *Promicromonospora* sp. (SE188) culture application on endogenous abscisic acid (ABA) and salicylic acid (SA) content. Double distilled water (DDW) and bacteria-free nutrient broth (NB) were used as controls. The different alphabetic letter indicates that treatments were significantly ($P<0.05$) different as evaluated by Duncan Multiple Range Test (DMRT). The error bar shows mean values ±standard deviation (n=3).

pared to DDW and NB control plants (Fig. 5). The ABA content in *Promicromonospora* sp. treated plants was 549.1 ng/gDW while the bacteria-free NB and DDW control plants had 614.6 ng/gDW and 632.7 ng/gDW. Salicylic acid content, on the other hand, was significantly higher in *Promicromonospora* sp. SE188 treated plants as compared to the DDW and NB control plants (Fig. 5). The content of SA in treated plants was 46.2 ng/gDW while in DDW and NB control plants it was 38.8 ng/gDW and 36.2 ng/gDW, respectively.

Discussion

Application of the *Promicromonospora* sp. SE188 culture proved to have a growth-promoting effect on tomato plants as compared to the bacteria-free broth and DDW controls. Plant growth-promotion by PGPR species able to produce gibberellins has been reported in several previous studies (Bastián *et al*., 1998; Gutiérrez-Manero *et al*., 2001). In a similar study, *Phaseolus lunatus* inoculated with a specific strain of *Bradyrhizobium* sp. showed a marked internode elongation that was not observed in plants inoculated with other bradyrhizobia (Dobert *et al*., 1992). Yanni *et al.* (2001) observed that the inoculation of rice with Rhizobium strains promoted seedling vigor, root length, shoot length, and grain yield of rice. They reported that pure cultures of these Rhizobium strains produced auxin (IAA) and gibberellins (tentatively identified as GA_7).

This growth-promotion capacity of *Promicromonospora* sp. SE188 might be attributed to its ability to produce gibberellins. There are various studies that suggested the influence of PGPR application on plant growth by synthesizing phytohormones (Lucy *et al*., 2004; Gulati *et al*., 2009). Tomato plants are sensitive to varying environmental conditions, and when treated with such a PGPR strain show improved plant growth as also shown in previous work (Yang *et al*., 2008). Microorganisms including fungi and rhizospheric bacteria, can produce various bioactive metabolites such as GAs, auxins, etc (Khan *et al*., 2011a, 2011b, 2011c). In the present study, we detected various GAs in the culture medium of *Promicromonospora* sp. SE188. This bacterium produced nine different GAs including physiologically active GA_1 and GA_4. This conforms with previous reports that rhizobacters can produce plant hormones. Previously, Kang *et al.* (2009) reported that a strain of *A. calcoaceticus* SE370 secreted ten different GAs into its growth environment, including bioactive GA_1, GA_3, and GA_4. Similarly, Joo *et al.* (2004) reported on 3b-hydroxylated GAs in *B. cereus* MJ-1, *B. macroides* CJ-29 and *B. pumilus* CJ-69. In *Azospirillum* sp., several studies have characterized gibberellins by capillary gas chromatography-mass spectrometry (GC-MS), specifically, GA_1, GA_3, GA_9, GA_{19}, and GA_{20} from gnotobiotic cultures of *A. lipoferum* (Bottini *et al*., 1989) and GA_1 and GA_3 from gnotobiotic cultures of *A. brasilense* (Janzen *et al*., 1992; Bottini *et al*., 2004). Similarly, Mansour *et al.* (1994) found that various strains of Streptomyces have the capacity to produce GA-like substances. GA analysis by HPLC coupled with GC-MS-SIM gave more reliable results when compared to TLC, bioassays or HPLC-UV which all had poor resolution and less reliability. The GAs were analyzed by GC/MS in selected ion monitoring (SIM) mode, which provides a more reliable GA quantification technique as compared to TLC, bioassays or HPLC-UV. The major advantage of GC/MS is its unbiased character. In comparison with non-MS detection methods based on chromatographic techniques (HPLC-DAD, GC-FID), where only compounds targeted by a special analytical protocol are found, GC-MS analyses can yield interesting and unexpected new information about a particular extract.

The process of traditional P fertilizer production is environmentally undesirable, not least because of the release of contaminants into the main product, gas stream and by-products (Song *et al*., 2008). Biological phosphate solubilization by active rhizobacters, on the other hand, provides additional support to plant vigor. Phosphate solubilization by *Promicromonospora* sp. SE188 was high, whereas the pH was low, after 96 h of incubation. We presume that the rhizobacteria secrete organic acids, which can play a role in phosphate solubilization. Kpomblekou and Tabatabai (1994) suggested that microorganisms that decrease the pH of culture medium during growth are efficient P solubilizers. Current results confirmed previous findings of Nautiyal *et al.* (2000), who reported that the maximum solubilization by bacterial strains was achieved after 3 days of incubation.

Endogenous plant growth hormones such as GAs, ABA, and SA play a vital role in plant growth and responses to them are of significant importance in understanding the acclimation mechanism of plants. Gibberellins are plant growth hormones specialized for plant growth and development, while ABA is a well-know plant stress hormone. Our study showed that the application of *Promicromonospora* sp. SE188 significantly promoted endogenous bioactive GA_4 and the immediate precursors of other bioactive GAs. The presence of GA_4 showed that the non-C-13 hydroxylation pathway was active during the interaction between tomato plants and rhizobacters. The level of GA_4 was significantly higher than the other GAs, suggesting that the major GA-biosynthesis pathway in tomatoes is the non-C-13 hydroxylation pathway. In the GA-biosynthesis pathway, GA_{12}-aldehyde is converted to GA_{12}, which is then either first oxidized at C-20 to form the C19 gibberellins GA_9, or 13-hydroxylated to give GA_{53}, which is oxidized at C-20 to produce GA_{20}. The final step in the formation of bioactive GAs in plants is the 3b-hydroxylation of GA_9 and GA_{53} to give GA_4 and GA_1, respectively (Hedden, 1997). On the other hand, the ABA level of tomato plants treated with *Promicromonospora* sp. SE188 was significantly lowered as compared to the NB and DDW controls. It is well understood that ABA levels increase in response to abiotic stress and can inhibit plant growth by decreasing the leaf area and shoot length (Khan *et al*., 2011a, 2011b, 2011c). A decrease in ABA levels in plants inoculated with *Promicromonospora* sp. SE188 suggests that the PGPR provides a favorable environment. Contrarily, SA was significantly higher in the treated plants as compared to the DDW and NB control plants. Salicylic acid often invokes oxidative responses and induces systemic acquired resistance against pathogenic attacks (Koch *et al*., 2000). Under abiotic stress, high endogenous SA may mitigate the negative effects of ROS accumulation. Such functions might counteract adverse effects on the bacteria-inoculated plants

as well (Gafur *et al*., 2004), while in a mutualistic relationship SA initiates induced systemic resistance (Pozo and Azcon-Aguilar, 2007). Alonso-Ramírez *et al*. (2009) have reported that GA-responsive genes and the exogenous addition of GAs are able to counteract the inhibitory effects of various adverse environmental conditions in seed germination and seedling growth of *Arabidopsis* through the modulation of SA biosynthesis. The same trend was also observed by Khan *et al*. (2011a), Iqbal and Ashraf (2010), and Navarro *et al*. (2008). Enhanced SA levels are especially important for the reduction of susceptibility of plants to biotic and abiotic stresses (Alonso-Ramírez *et al*., 2009).

In conclusion, our study suggests that *Promicromonospora* sp. SE188 is a novel PGPR due to its capacity to promote plant growth and metabolism, and increase the levels of the plant's endogenous ABA, SA, and GAs. In addition to producing various physiologically active and inactive gibberellins, the strain has the capacity to solubilize phosphate. The strain shows favorable effects on tomato plant growth, which suggests that broader field trails, testing it as a biofertilizer for higher crop production in eco-friendly farming systems, would be desirable.

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